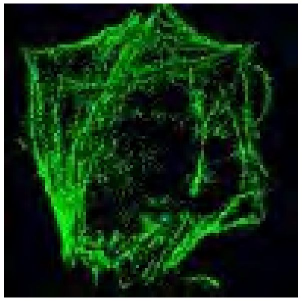
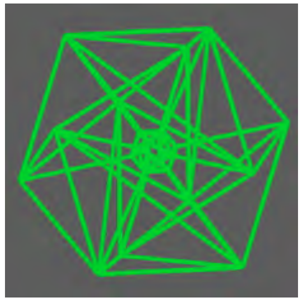
4.4 the cytoskeleton - tensegrity model





day	date		topic
tue	apr	03	introduction I - cell biology
thu	apr	05	introduction II - cytoskeletal biology, stem cells
tue	apr	10	introduction III - structural mechanics
thu	apr	12	biopolymers I - energy, tension, bending
thu	apr	12	homework I - biopolymers, directed stem cell differentiation
tue	apr	17	biopolymers II - entropy, FJC and WLC model
thu	apr	19	biopolymers III - polymerization kinetics in amoeba
tue	apr	24	cytoskeletal mechanics I - fiber bundle model for filopodia
thu	apr	26	cytoskeletal mechanics II - network model for red blood cells
thu	apr	26	homework II - cytoskeleton, cell mechanics challenges
tue	may	01	cytoskeletal mechanics III - tensegrity model for generic eukaryotic cells
thu	may	03	biomembranes I - micropipette aspiration in white blood cells and cartilage cells
tue	may	08	biomembranes II - lipid bilayer, soap bubble, cell membrane
thu	may	10	biomembranes III - energy, tension, shear, bending
tue	may	15	mechanotransduction I - inter- and intracellular signaling, bone cells
tue	may	15	homework III - micropipette aspiration, final project
thu	may	17	summary and midterm preparation
tue	may	22	midterm
thu	may	24	mechanotransduction II - electrophysiology in nerve cells
tue	may	29	mechanotransduction III - excitation contraction in skeletal muscle and heart cells
thu	may	31	final projects I - oral presentations
tue	jun	05	final projects II - oral presentations
thu	jun	07	no class
fri	jun	08	final projects - written projects due

from molecular level to cellular level

assuming we know the mechanical properties of the individual filaments, what does that actually tell us about the assembly of filaments that we find in the cell?

- could we then predict the **stiffness of the overall assembly**?
- how does the filament microstructure affect **cytoskeletal properties**?
- how can we calculate the **macroscopic network properties** from the individual microscopic filament properties?

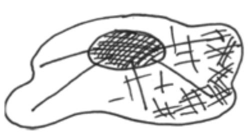
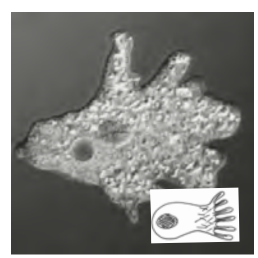


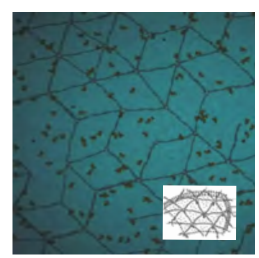
Figure 4.1: The cytoskeleton provides structural stability and is responsible for forces during cell locomotion. Microtubules are thick hollow cylinders reaching out from the nucleus to the membrane, intermediate filaments can be found anywhere in the cytosol, and actin filaments are usually concentrated close to the cell membrane.

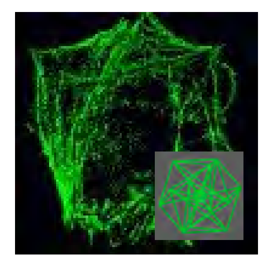
from molecular level to cellular level

three examples

- **fiber bundle model** for filopodia
- **network model** for red blood cell membranes
- **tensegrity model** for generic cell structures







red blood cells

erythrocytes, red blood cells are essential to deliver oxygen to the body via the blood flow through the circulatory system. they take up oxygen in the lungs and release it while squeezing through the body's capillaries. adult humans have about 2-3 10^{13}, 20-30 trillion, red blood cells comprising about a quarter of the total amount of cells in the human body.

network model for red blood cells

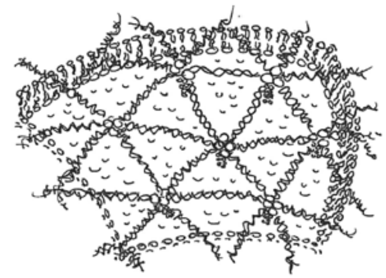


Figure 4.6: Microstructural architecture of the cell membrane of a red blood cell. A six-fold connected network of spectrin tetramers which are crosslinked through short actin filaments, anchored to the phospholipid bilayer, provides structural support to the inner cell membrane.

homogenization - hill-mandel condition

aim. to determine the overall material properties κ and μ of the network of spectrin chains in terms of the spectrin chain stiffness k

ENERGY APPROACH

$$W^{\mathrm{mac}} \doteq W^{\mathrm{mic}}$$

It has been shown how the central problem is reducible to the calculation of average stress or strain in one or other phase. A more versatile approach stems directly from classical theorems in elasticity and focusses attention on strain energies.

hill, r. elastic properties of reinforced solids: some theoretical principles, journal of the mechanics and physics of solids, 1963, 11:357–372.

different network kinematics

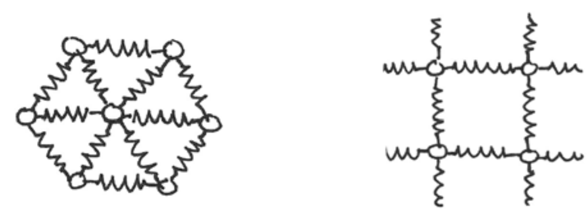


Figure 4.8: Microstructural architecture of a six-fold and four-fold connected network. The theory of homogenization helps to explain why nature prefers a six-fold connected network geometry.

single spring energy

free energy $W^{\rm spr}$ of a single spring

$$W^{\rm spr} = \frac{1}{2}\,k\,\delta^2 = \frac{1}{2}\,k\,[\,l - l_0\,]^2 \qquad \text{where} \qquad \delta = l - l_0$$

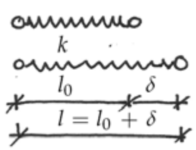
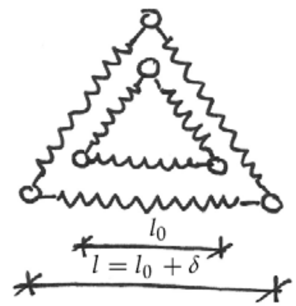


Figure 4.7: Spectrin can be modeled as Gaussian chain which we can conceptually replace by an equivalent linear entropic spring with a spring stiffness of $k = 3\,\mathrm{k}\,T\,N\,/\,L$. The strain energy of this spring can then be expressed as $W^{\rm spr} = \frac{1}{2}\,k\,\delta^2$.

discrete microscopic network energy

extension



$$h_0 = \frac{1}{2}\sqrt{3}\,l_0$$

$$W^{\rm mic} = \frac{\sum_{i=1}^3 W_i^{\rm spr}}{\sum_{i=1}^3 A_i^{\rm spr}}$$

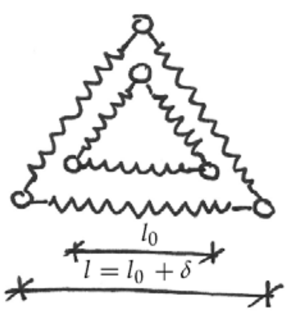
$$\textstyle\sum_{i=1}^3 W_i^{\rm spr} = 3\,W^{\rm spr} = 3\,[\,\frac{1}{2}\,k\,\delta^2]$$

$$\textstyle\sum_{i=1}^3 A_i^{\rm spr} = 3\,A^{\rm spr} = \frac{1}{2}\sqrt{3}\,l_0^2$$

$$W^{\rm mic} = \frac{3\,\frac{1}{2}\,k\,\delta^2}{\frac{1}{2}\sqrt{3}\,l_0^2} = \sqrt{3}\,k\left[\frac{\delta}{l_0}\right]^2$$

equivalent macroscopic energy

extension



$$W^{\rm mac} = \frac{1}{2}\,\kappa\,[\,\varepsilon_{xx} + \varepsilon_{yy}\,]^2 + \frac{1}{2}\,\mu\,[\,\varepsilon_{xx} - \varepsilon_{yy}\,]^2 + 2\,\mu\,\varepsilon_{xy}^2$$

micro-to-macro kinematics

$$\varepsilon_{xx} = \varepsilon_{yy} = \delta\,/\,l_0 \qquad \varepsilon_{xy} = 0$$

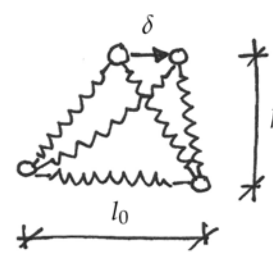
$$W^{\rm mac} \doteq W^{\rm mic}$$

$$\frac{1}{2}\,\kappa\left[\frac{\delta}{l_0} + \frac{\delta}{l_0}\right]^2 = \sqrt{3}\,k\left[\frac{\delta}{l_0}\right]^2$$

$$\underline{\underline{\kappa = \frac{1}{2}\sqrt{3}\,k}}$$

discrete microscopic network energy

shear



$$h_0 = \frac{1}{2}\sqrt{3}\,l_0$$

$$W^{\rm mic} = \frac{\sum_{i=1}^3 W_i^{\rm spr}}{\sum_{i=1}^3 A_i^{\rm spr}}$$

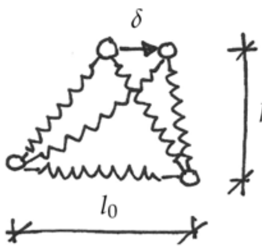
$$\textstyle\sum_{i=1}^3 W_i^{\rm spr} = \underbrace{\frac{1}{2}\,k\,[\,+\frac{1}{2}\delta\,]^2}_{\text{left spring}} + \underbrace{\frac{1}{2}\,k\,[\,-\frac{1}{2}\delta\,]^2}_{\text{right spring}} + \underbrace{0}_{\text{lower spring}} = \frac{1}{4}\,k\,\delta^2$$

$$\textstyle\sum_{i=1}^3 A_i^{\rm spr} = 3\,A^{\rm spr} = \frac{1}{2}\sqrt{3}\,l_0^2$$

$$W^{\rm mic} = \frac{\frac{1}{4}\,k\,\delta^2}{\frac{1}{2}\sqrt{3}\,l_0^2} = \frac{\sqrt{3}}{6}\,k\left[\frac{\delta}{l_0}\right]^2$$

equivalent macroscopic energy

shear



$h_0 = \frac{1}{2}\sqrt{3}\, l_0$

$$W^{\text{mac}} = \tfrac{1}{2}\,\kappa\,[\,\varepsilon_{xx} + \varepsilon_{yy}\,]^2 + \tfrac{1}{2}\,\mu\,[\,\varepsilon_{xx} - \varepsilon_{yy}\,]^2 + 2\,\mu\,\varepsilon_{xy}^2$$

micro-to-macro kinematics

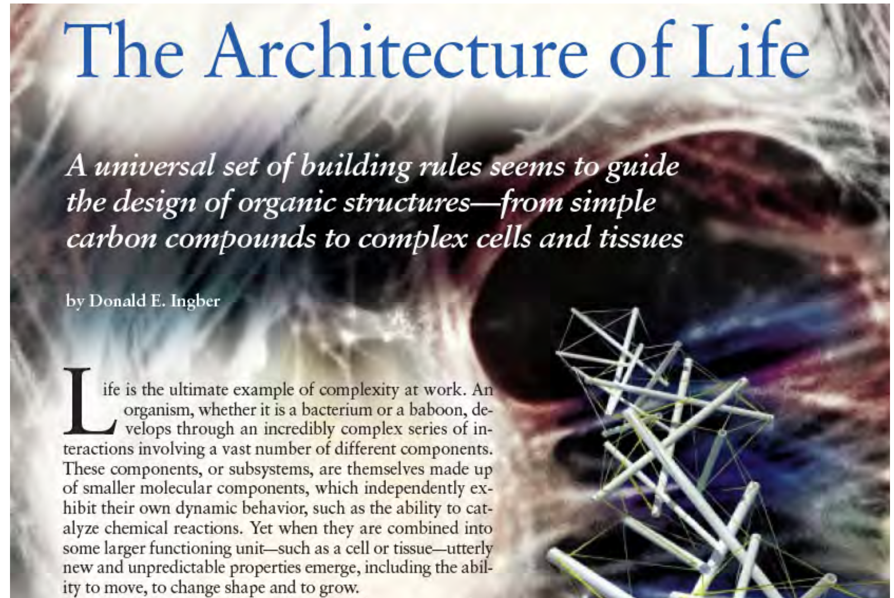
$$\varepsilon_{xx} = 0 \qquad \varepsilon_{yy} = 0$$

$$\varepsilon_{xy} = \frac{1}{2}\left[\frac{\delta}{\frac{1}{2}\sqrt{3}\,l_0} + 0\right] = \frac{1}{\sqrt{3}}\,\frac{\delta}{l_0}$$

$$W^{\text{mac}} \doteq W^{\text{mic}}$$

$$2\,\mu\left[\frac{1}{\sqrt{3}}\,\frac{\delta}{l_0}\right]^2 = \frac{\sqrt{3}}{6}\,k\left[\frac{\delta}{l_0}\right]^2$$

$$\underline{\underline{\mu = \tfrac{1}{4}\sqrt{3}\,k}}$$



The Architecture of Life

A universal set of building rules seems to guide the design of organic structures—from simple carbon compounds to complex cells and tissues

by Donald E. Ingber

Life is the ultimate example of complexity at work. An organism, whether it is a bacterium or a baboon, develops through an incredibly complex series of interactions involving a vast number of different components. These components, or subsystems, are themselves made up of smaller molecular components, which independently exhibit their own dynamic behavior, such as the ability to catalyze chemical reactions. Yet when they are combined into some larger functioning unit—such as a cell or tissue—utterly new and unpredictable properties emerge, including the ability to move, to change shape and to grow.

tensegrity = tension + integrity

the term tensegrity was first coined by buckminster fuller to describe a structure in which **continuous tension** in its members forms the **basis for structural integrity**. fuller most famously demonstrated the concept of tensegrity in architecture through the **design of geodesic domes** while his student, the artist kenneth snelson, applied the concept of tensegrity to creating sculptures that appear to defy gravity. snelson's tensegrity sculptures are minimal in components and achieve their stability through dynamic distribution of tension and compression forces amongst their members to create internal balance. it was upon viewing snelson's art that donald ingber became inspired by the sculpture's structural efficiency and dynamic force balance to **adopt tensegrity as a paradigm** upon which to **analyze cell structure** and mechanics. it has been 30 years since the premier appearance of the cellular tensegrity model. although the model is still largely under discussion, empirical evidence suggests that the model may explain a wide variety of phenomena ranging from tumor growth to cell motility.

tensegrity = tension + integrity

tensegrity bike held together by wires

lloyd alter [2009]

example - geodesic domes

geodesic domes carry load with minimum material

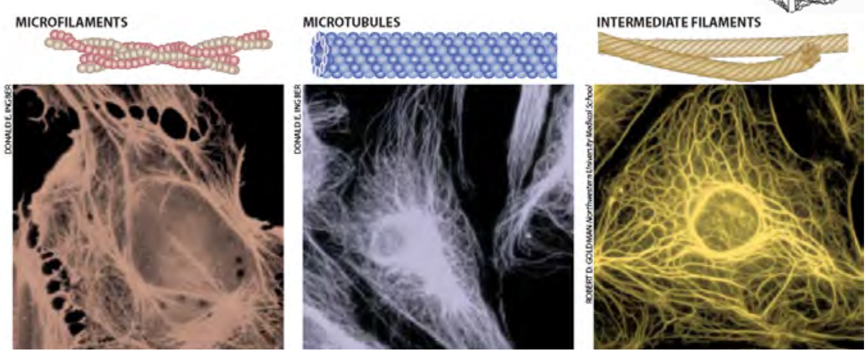
ingber [1998]

example - geodesic domes

pollen grains are geodesic domes

ingber [1998]

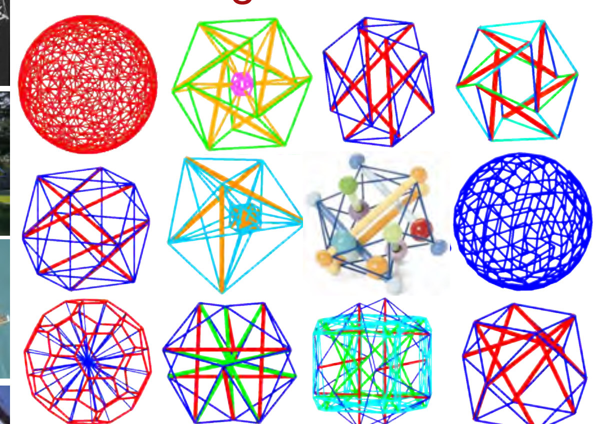
tensegrity = tension + integrity

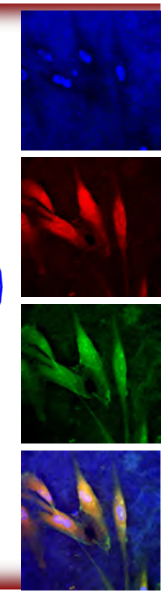


balanced interplay between tension and compression

ingber [1998]

cell design contest 2007

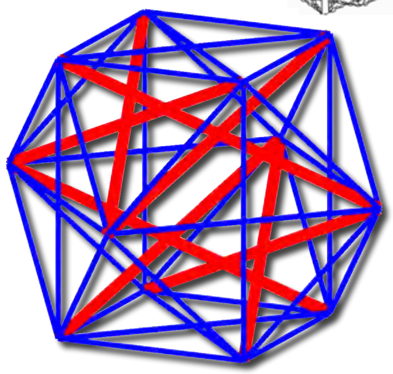




joey doll, emily gu,lizzie hager-barnard, zubin huang, amir ali kia, monica ortiz, bryan petzold, yufen shi, sang do suk, takane usui, chun hua zheng, sonke carstens, ron kwon, chris jacobs, oscar abilez, jennifer blundo, jayakumar rajadas, beth pruitt

bryan's cell…

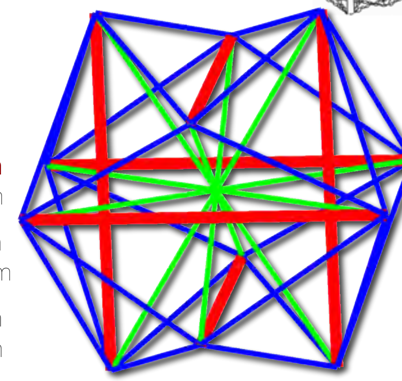
- number of microtubules 8
- number of filaments 36
- fiber length 27.4135 d^{cell}
- volume fraction 0.00755 V^{cell}
- tensile stiffness 0.488149N/nm
  $k^{ten} = F^{ten}/u$ 1.176537N/nm
- compressive stiffness 4.86e-11N/nm
  $k^{com} = F^{com}/u$ -0.19328N/nm
- shear stiffness 4.91e-05N/nm
  $k^{shr} = F^{shr}/u$ 0.009783N/nm



… is super stiff and yet compliant

lizzie's cell

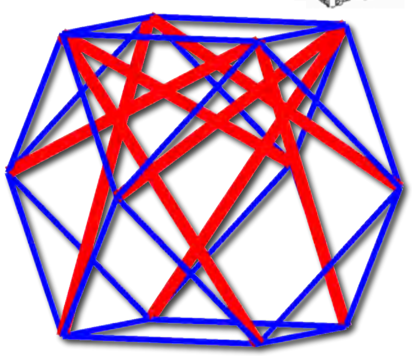
- number of microtubules 6
- number of filaments 36
- fiber length 23.7215 d^{cell}
- volume fraction 0.00609 V^{cell}
- tensile stiffness 0.145106N/nm
  $k^{ten} = F^{ten}/u$ 0.165106N/nm
- compressive stiffness 0.000000N/nm
  $k^{com} = F^{com}/u$ -0.006020N/nm
- shear stiffness 0.024453N/nm
  $k^{shr} = F^{shr}/u$ 0.050152N/nm



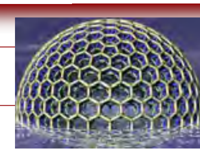
… is a typical tensegrity structure

takane's cell

- number of microtubules 8
- number of filaments 24
- fiber length 28.9282 d^{cell}
- volume fraction 0.00630 V^{cell}
- tensile stiffness 0.388568N/nm
  $k^{ten} = F^{ten}/u$ 0.776480N/nm
- compressive stiffness 0.581394N/nm
  $k^{com} = F^{com}/u$ 0.714010N/nm
- shear stiffness 0.016585N/nm
  $k^{shr} = F^{shr}/u$ 0.051590N/nm

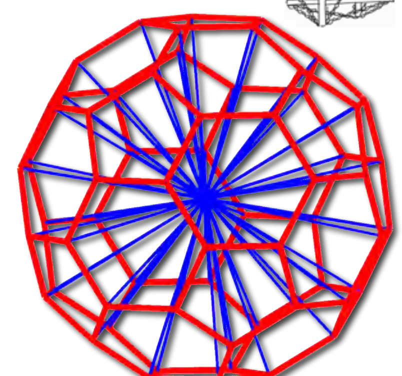


… is modeled after a sculpture and really cool



lizzie's cell

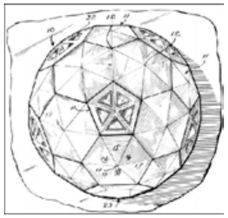
- number of microtubules 90
- number of filaments 60
- fiber length 48.1597 d^{cell}
- volume fraction 0.03099 V^{cell}
- tensile stiffness 0.000000N/nm
  $k^{ten} = F^{ten}/u$ 0.000000N/nm
- compressive stiffness 0.000000N/nm
  $k^{com} = F^{com}/u$ 0.000000N/nm
- shear stiffness 0.000000N/nm
  $k^{shr} = F^{shr}/u$ 0.000000N/nm



… looks really cool but has no stiffness at all

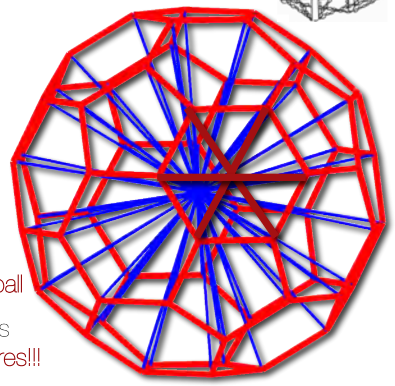
lizzie's cell

- number of microtubules 90
- number of filaments 60
- fiber length 48.1597 d^{cell}
- volume fraction 0.03099 V^{cell}



tensile stiffness
prestress! example ball

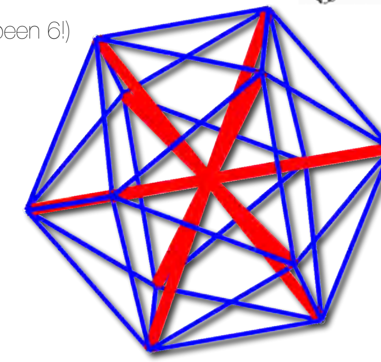
compressive stiffness
triangular substructures!!!



… needs triangular substructures for support

amir's cell

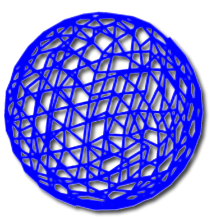
- number of microtubules 12 (should have been 6!)
- number of filaments 30
- fiber length 21.7719 d^{cell}
- volume fraction 0.00624 V^{cell}
- tensile stiffness 0.000000N/nm
  $k^{ten} = F^{ten}/u$ 0.000000N/nm
- compressive stiffness 0.000000N/nm
  $k^{com} = F^{com}/u$ 0.000000N/nm
- shear stiffness 0.000000N/nm
  $k^{shr} = F^{shr}/u$ 0.000000N/nm



… typical structure that needs prestress

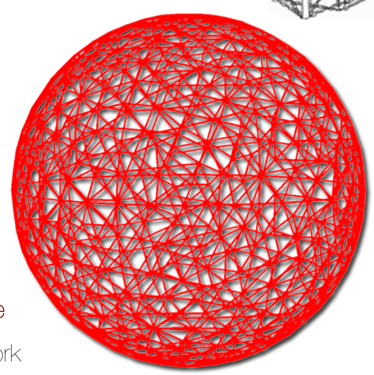
zubin's and joey's cells

- number of microtubules 607
- number of filaments 1815
- fiber length 145.3161 d^{cell}
- volume fraction 0.093529 V^{cell}



different cell type
membrane structure

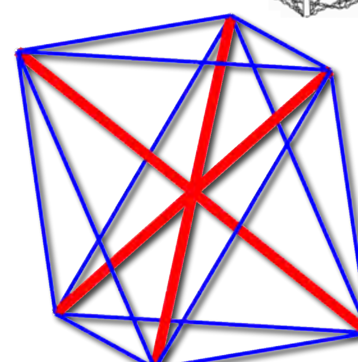
five- or sixfold network



… membrane models

chunhua's cell

- number of microtubules 3
- number of filaments 62
- fiber length 11.4853 d^{cell}
- volume fraction 0.00321 V^{cell}
- tensile stiffness 0.164315N/nm
  $k^{ten} = F^{ten}/u$ 1.526569N/nm
- compressive stiffness $6.31\ 10^{-11}$N/nm
  $k^{com} = F^{com}/u$ -1.18324N/nm
- shear stiffness $1.51\ 10^{-10}$N /nm
  $k^{shr} = F^{shr}/u$ 0.079761N/nm



… and the winner is: the smallest tensegrity structure

Proceedings of the ASME 2008 Summer Bioengineering Conference (SBC2008)
June 25-29, Marriott Resort, Marco Island, Florida, USA

SBC2008-192407

**EXPLORING CELLULAR TENSEGRITY:
PHYSICAL MODELING AND COMPUTATIONAL SIMULATION**

Chun hua Zheng[*], Joseph Doll[*], Emily Gu[†], Elizabeth Hager-Barnard[‡], Zubin Huang[*], AmirAli Kia[*], Monica Ortiz[†], Bryan Petzold, Yufen Shi, Sang Do Suk[*], Takane Usui[*], Ronald Kwon[*], Christopher Jacobs[*†], Ellen Kuhl[*†]

Department of Mechanical Engineering[*]
Department of Materials Science and Engineering[‡]
Department of Bioengineering[†]
Stanford University, Stanford, CA 94305, USA

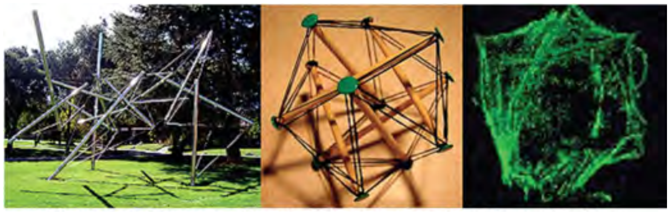
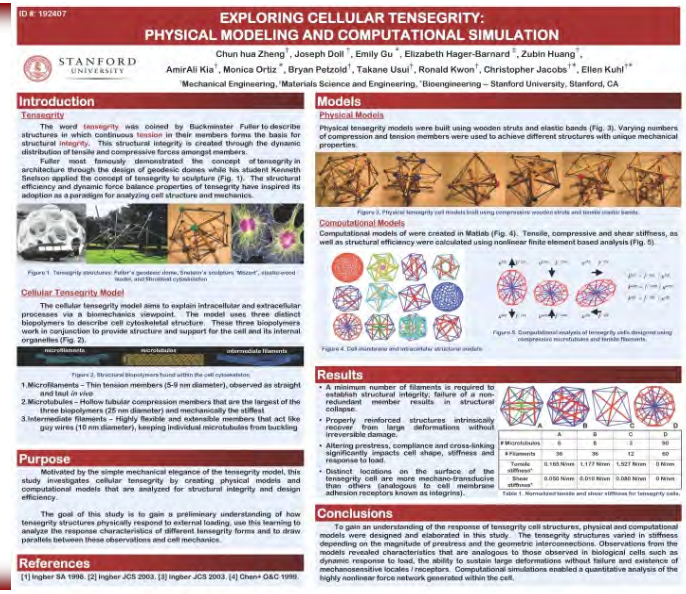


figure 1. tensegrity structures. snelson's sculpture `mozart' on stanford campus, wood-rubber model, and cytoskeleton of the cell.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**EXPLORING CELLULAR TENSEGRITY:
PHYSICAL MODELING AND COMPUTATIONAL SIMULATION**

STANFORD UNIVERSITY

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[†]Mechanical Engineering, [‡]Materials Science and Engineering, [*]Bioengineering – Stanford University, Stanford, CA

Introduction

Tensegrity

The word tensegrity was coined by Buckminster Fuller to describe structures in which continuous tension in their members forms the basis for structural integrity. This structural integrity is created through the dynamic distribution of tensile and compressive forces amongst members.

Fuller most famously demonstrated the concept of tensegrity in architecture through the design of geodesic domes while his student Kenneth Snelson applied the concept of tensegrity to sculpture (Fig. 1). The structural efficiency and dynamic force balance properties of tensegrity have inspired its adoption as a paradigm for analyzing cell structure and mechanics.

Figure 1. Tensegrity structures: Fuller's geodesic dome, Snelson's sculpture 'Mozart', elastic-wood model, and fibroblast cytoskeleton

Cellular Tensegrity Model

The cellular tensegrity model aims to explain intracellular and extracellular processes via a biomechanics viewpoint. The model uses three distinct biopolymers to describe cell cytoskeletal structure. These three biopolymers work in conjunction to provide structure and support for the cell and its internal organelles (Fig. 2).

microfilaments microtubules intermediate filaments

Figure 2. Structural biopolymers found within the cell cytoskeleton

1. Microfilaments – Thin tension members (5-9 nm diameter), observed as straight and taut *in vivo*
2. Microtubules – Hollow tubular compression members that are the largest of the three biopolymers (25 nm diameter) and mechanically the stiffest
3. Intermediate filaments – Highly flexible and extensible members that act like guy wires (10 nm diameter), keeping individual microtubules from buckling

Purpose

Motivated by the simple mechanical elegance of the tensegrity model, this study investigates cellular tensegrity by creating physical models and computational models that are analyzed for structural integrity and design efficiency.

The goal of this study is to gain a preliminary understanding of how tensegrity structures physically respond to external loading, use this learning to analyze the response characteristics of different tensegrity forms and to draw parallels between these observations and cell mechanics.

References

[1] Ingber SA 1998. [2] Ingber JCS 2003. [3] Ingber JCS 2003. [4] Chen+ O&C 1999.

Models

Physical Models

Physical tensegrity models were built using wooden struts and elastic bands (Fig. 3). Varying numbers of compression and tension members were used to achieve different structures with unique mechanical properties.

Figure 3. Physical tensegrity cell models built using compressive wooden struts and tensile elastic bands.

Computational Models

Computational models of were created in Matlab (Fig. 4). Tensile, compressive and shear stiffness, as well as structural efficiency were calculated using nonlinear finite element based analysis (Fig. 5).

Figure 4. Cell membrane and intracellular structural models

Figure 5. Computational analysis of tensegrity cells designed using compressive microtubules and tensile filaments.

Results

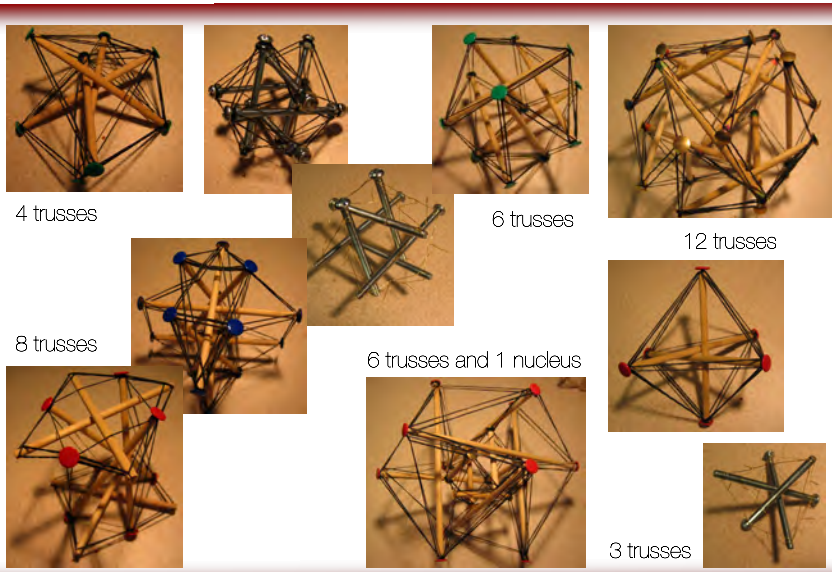
- A minimum number of filaments is required to establish structural integrity; failure of a non-redundant member results in structural collapse.
- Properly reinforced structures intrinsically recover from large deformations without irreversible damage.
- Altering prestress, compliance and cross-linking significantly impacts cell shape, stiffness and response to load.
- Distinct locations on the surface of the tensegrity cell are more mechano-transducive than others (analogous to cell membrane adhesion receptors known as integrins).

	A	B	C	D
# Microtubules	6	6	3	90
# Filaments	36	36	12	60
Tensile stiffness*	0.165 N/nm	1.177 N/nm	1.527 N/nm	0 N/nm
Shear stiffness*	0.050 N/nm	0.010 N/nm	0.080 N/nm	0 N/nm

Table 1. Normalized tensile and shear stiffness for tensegrity cells.

Conclusions

To gain an understanding of the response of tensegrity cell structures, physical and computational models were designed and elaborated in this study. The tensegrity structures varied in stiffness depending on the magnitude of prestress and the geometric interconnections. Observations from the models revealed characteristics that are analogous to those observed in biological cells such as dynamic response to load, the ability to sustain large deformations without failure and existence of mechanosensitive locales / receptors. Computational simulations enabled a quantitative analysis of the highly nonlinear force network generated within the cell.



4 trusses

6 trusses

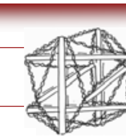
12 trusses

8 trusses

6 trusses and 1 nucleus

3 trusses

tensegrity models for cells



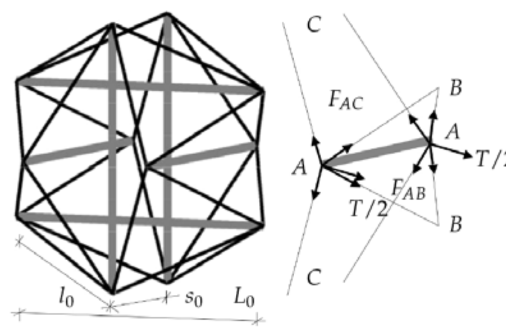
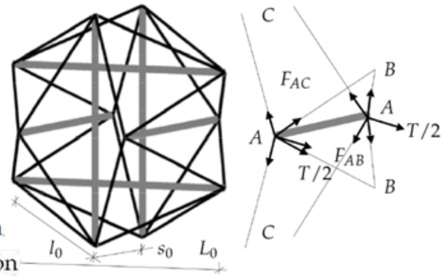


Figure 4.12: Kinematics of simple tensegrity cell model consisting of six compressive trusses (grey) and 24 tensile ropes (black). In the original state, all trusses are of the same length L_0, the rope lengths are $l_0 = \sqrt{3/8}\,L_0$, and the distances between two parallel trusses are $s_0 = 1/2\,L_0$.

tensegrity models for cells

- kinematics $\quad l_0^2 = \left[\frac{L_0 - s_0}{2}\right]^2 + \left[\frac{s_0}{2}\right]^2 + \left[\frac{L_0}{2}\right]^2 \to l_0 = \frac{1}{2}\sqrt{[L_0 - s_0]^2 + s_0^2 + L_0^2}$
- equilibrium $\quad \sum F \doteq 0: \quad T + 4\,F_{AB}\left[\frac{L_0 - s_0}{2\,l_0}\right] - 4\,F_{AC}\left[\frac{s_0}{2\,l_0}\right] = 0$
- constitutive equation $\quad F = k\,[\,l - l_r\,]$



$T = 0$ special case

$s_0 = L_0 \,/\, 2$ from the equilibrium equation

$l_0 = \sqrt{3\,/\,8} L_0$ from the kinematic equation

discrete microscopic network energy

- hill condition and its derivative wrt deformed truss distance s_x

$$W^{\text{mac}} \doteq W^{\text{mic}} \quad \text{or} \quad \frac{\partial W^{\text{mac}}}{\partial s_x} \doteq \frac{\partial W^{\text{mic}}}{\partial s_x}$$

- microscopic free energy density

$$W^{\text{mic}} = \frac{1}{V_0}\int_{s_0}^{s_x} T\,\mathrm{d}x \quad \text{thus} \quad \frac{\partial W^{\text{mic}}}{\partial s_x} = \frac{T}{V_0}$$

tensile force T acting along the changing length $\int_{s_0}^{s_x} \mathrm{d}x$ scaled by volume of the tensegrity cell V_0

equivalent macroscopic energy

- macroscopic free energy

$$W^{\text{mac}} = \frac{1}{2}\,\varepsilon\,E\,\varepsilon \quad \text{thus} \quad \frac{\partial W^{\text{mac}}}{\partial s_x} = \frac{\partial W^{\text{mac}}}{\partial \varepsilon}\frac{\partial \varepsilon}{\partial s_x} = E\,\varepsilon\,\frac{\partial \varepsilon}{\partial s_x}$$

- mirco-to-macro kinematics / strain

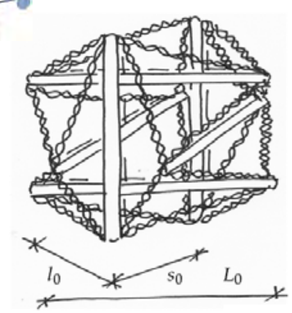
$$\varepsilon = \frac{s_x - s_0}{s_0} \quad \text{such that} \quad \frac{\partial \varepsilon}{\partial s_x} = \frac{1}{s_0}$$

- hill condition and its derivative wrt deformed truss distance s_x

$$W^{\text{mac}} \doteq W^{\text{mic}} \quad \text{or} \quad \frac{\partial W^{\text{mac}}}{\partial s_x} \doteq \frac{\partial W^{\text{mic}}}{\partial s_x} \qquad E = \frac{s_0\,T}{\varepsilon\,V_0}$$

$$E = \frac{2\sqrt{3}}{5\sqrt{2}l_0}\frac{T}{s_x - s_0} \quad \text{small strain} \quad E_0 = 5.85\,\frac{F_0}{l_0^2}\frac{1 + 4\,\varepsilon_0}{1 + 12\varepsilon_0}$$

tensegrity models for cells



E_0 ... incremental modulus

F_0 ... resting force in actin filaments

L_0 ... length of microtubules

l_0 ... resting length of actin filaments

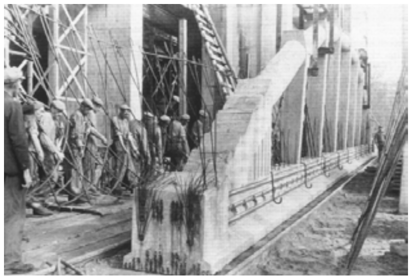
ε_0 ... strain in actin filaments

$$W^{\text{mac}} \doteq W^{\text{mic}} \qquad W^{\text{mac}} = \frac{1}{2}\,\varepsilon\,E\,\varepsilon \qquad W^{\text{mic}} = \frac{1}{V_0}\int_{s_0}^{s_x} T\,\mathrm{d}x$$

$$E = \frac{2\sqrt{3}}{5\sqrt{2}l_0}\frac{T}{s_x - s_0} \quad \text{small strain} \quad E_0 = 5.85\,\frac{F_0}{l_0^2}\frac{1 + 4\,\varepsilon_0}{1 + 12\varepsilon_0}$$

tensegrity models for prestress

prestress. tensegrity models are an extremely elegant way to model prestress through the application of initial **tension in the rope members**. in fact prestress is inherent to tensegrity structures in that they stabilize themselves through their own weight balanced by prestress. prestress, very **common to biological structures**, is a design concept that we have adopted from nature, for example in the form of prestressed reinforced concrete. prestressed concrete was patented by a san francisco engineer in 1886.



prestress - analytically predicted

- assume prestress is approximately equal in all three directions

$P \approx \frac{1}{3} \nu^{\text{actin}} \sigma^{\text{actin}}$

- volume fraction of actin filaments

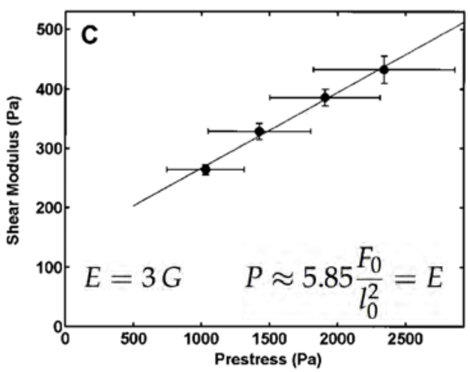
$$\nu^{\text{actin}} = \frac{V^{\text{actin}}}{V_0} = \frac{24 A^{\text{actin}} l_0}{[5\sqrt{2}]/[3\sqrt{3}] l_0^3} = \frac{24 A^{\text{actin}}}{1.3608 l_0^2}$$

- stress in a typical actin filament $\sigma^{\text{actin}} = \frac{F_0}{A^{\text{actin}}}$
- approximation of prestress

$$P \approx \frac{1}{3} \nu^{\text{actin}} \sigma^{\text{actin}} = \frac{1}{3} \frac{24 \, A^{\text{actin}}}{1.3608 l_0^2} \frac{F_0}{A^{\text{actin}}} \qquad P \approx 5.85 \frac{F_0}{l_0^2} = E$$

prestress is of the same order as young's modulus

prestress - experimentally measured



prestress is of the same order as young's modulus

wang, naruse, stamenovic, fredberg, mijailovich, tolic-norrelykke, polte, mannix, ingber [2001]

tensegrity structures on campus

lightweight and strong

snelson [1966]